



ON THE MORPHOLOGY AND SYSTEMATIC POSITION
OF THE FAMILY *MICROPTERYGIDÆ* (SENS. LAT.).

INTRODUCTION AND PART I. (THE WINGS).

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(Plate iii. and fourteen Text-figures).

In carrying out my researches on the Panorpid Complex (9, 10), it was necessary to study very carefully the remarkable family of archaic Moths known as the *Micropterygidae*, since these are supposed to represent the oldest existing types of Lepidoptera. The results obtained would, under ordinary circumstances, have been included, piece by piece, in the various parts of my work on the Panorpid Complex, and would have been used simply as part of the evidence in the more general problem of the relationships of the Orders composing the Complex.

However, during the last year, two events have occurred which appear to me to make it essential that a more exhaustive study of this interesting family should be undertaken, with the special object of determining, as exactly as possible, its true relationships and systematic position. These events are: firstly, the receipt of a paper by Dr. T. A. Chapman, M.D., F.R.S., in which (2) he definitely removes the genus *Micropteryx* itself from the rest of the *Micropterygidae*, and proposes for it a new Order Zeugloptera; and, secondly, the receipt of Professor Comstock's new book on the Wings of Insects (3), in which he removes the whole family *Micropterygidae* from the Lepidoptera, and places them in the Trichoptera as a new Suborder, the Micropterygina or Terrestrial Trichoptera, of equal value with the Phryganeina or Aquatic Trichoptera, which includes all the Trichoptera as usually understood by entomologists.

My own research, in which the presence of the frenulum in

all *Micropterygidae* was demonstrated(9), was first published before I received either of the above works; in actual date of publication (March, 1918) it was later than Dr. Chapman's paper, but earlier than Professor Comstock's book. The dates of all three were, however, close enough together to prevent the knowledge contained in any one of them from being used by either of the other authors. Had this been possible, I do not doubt that the views of each of us would have been profoundly modified by the work of the other two.

As instances of this, I would mention the unfortunate selection of the name *Zeugloptera* for the new Order proposed by Dr. Chapman. The name was suggested by Mr. Durrant, from the Greek ζεύγλον = jugum. Had either Dr. Chapman or Mr. Durrant known of the existence of the frenulum in these insects, this name, at any rate, must have been barred; as it is, it is a most unfortunate choice. Again, Professor Comstock says, in justification of his removal of the *Micropterygidae* to the Order Trichoptera(3, p.318): —“If the *Micropterygidae* be retained in the order Lepidoptera, they must be considered the most generalised members of the order, being near the stem form from which the Trichoptera and the Lepidoptera have been evolved. This view necessitates the explanation of the manner in which the *Hepialidae*, with their peculiar jugum, and the Frenatæ were evolved from a form having a well-developed fibula, like that of *Mnemonica* and *Rhyacophila*. This must be done if the Lepidoptera, including the *Micropterygidae*, is to be shown to be a monophylitic group.” As the explanation here asked for was actually given in my work on the Panorpoid Complex, Part i.(9), it is quite clear that Professor Comstock's decision would have been materially affected if my paper had been available to him. On the other hand, my own results would have been altered to some extent, if I had had access to his account of the jugal lobe of *Mnemonica* (3, p.315), a genus of which I had very little material.

The *Micropterygidae* have long been of especial interest to entomologists, but it does not appear that any study of their internal organs has yet been carried out; and the present condition of our knowledge of the family is wholly due to the study

of set specimens, of cleared mounts of the wings and of the mouth-parts. The same is true of those larval and pupal forms known. Thanks to the labours of Dr. Chapman, the complete life-history of the genus *Eriocrania* is known; while, in the genus *Micropteryx*, the same indefatigable worker has succeeded several times in rearing the insect from the egg as far as the last larval instar, though, so far, baffled in obtaining the pupa. The larva and pupa of the genus *Mnemonica* are known: they are closely related to those of *Eriocrania*.

The differences between the larva of *Micropteryx*, on the one hand, and those of *Eriocrania* and *Mnemonica* on the other, are so great as almost to justify in themselves Dr. Chapman's original separation of the family *Micropterygidae* (sens. lat.) into the two families *Micropterygidae* (s.str.) and *Eriocraniidae*(1). If we take into account also the differences in the mouth-parts of the imagines, this separation is surely justified entirely. Nevertheless, in entering upon the discussion with which this paper has to deal, I have felt it advisable to follow Meyrick in treating these insects as a single group, provisionally taken as of family rank, merely for convenience of title, and for facilitating the discussion itself. Whether they belong to one family or two, to one Order or two, or to what Order they are to be relegated, it is the purpose of this paper to try to discover. Hence, in the title, I speak of them simply as the *Micropterygidae* (sens. lat.), without prejudicing the case by indicating that this group belongs to any definite Order of Insects.

The receipt of Dr. Chapman's paper(2), and my own discoveries, so stimulated my interest in this group that I proceeded to get into touch with Dr. Chapman himself by correspondence, and asked him whether he could assist me to carry out a full biological study of it. Less than a year has passed since this correspondence, already so fruitful of results for me, was inaugurated; and I find it hard to realise that the fine collection of material now in my hands is the result of so short a period of contact with Dr. Chapman's wonderful generosity and kindness. I feel that no words of thanks of mine can possibly convey to him my deep appreciation of what he has done; nevertheless, I here

express my profound gratitude and thanks to him, and trust that the results which he has made possible, by his unselfish and painstaking supplying of the requisite material, may be in themselves the best acknowledgment of my deep debt to him. In saying this, I have in mind especially the fact that he knew, from my first letter, how disinclined I was to accept his removal of the genus *Micropteryx* from its (as I hold) nearly related genera to a new Order; yet, knowing this, he has not spared himself, at his age, in obtaining for me all the rare material which he, and nobody else in the world, is able to secure, as the result of many years untiring study of this group. One would have to search far indeed for a finer example of the true scientific spirit, in which one's own conclusions, however dear they may be on account of the work and sacrifices which gave them birth, are nevertheless not considered at all, when there is a possibility of supplying another scientist, holding perhaps opposite views, with the material for carrying out his researches.

That I have not overstated the case it is now my pleasure to prove, by an enumeration of the various consignments of material which I have already received from Dr. Chapman. The first consignment was sent off in January of this year (1918); the last was received last month (Nov., 1918), and more are promised. Of more than a dozen consignments altogether, only one (the second) has been lost by the action of submarines. The following is a list of the material so far received, on which this paper is chiefly written:—

(1) Dried cocoons and pupæ of *Eriocrania semipurpurella* Steph.

(2) Slides of the exoskeleton of the last larval instar of *Eriocrania semipurpurella*.

(3) A slide of the exoskeleton of the first larval instar of *Micropteryx calthella* Linn.

(The lost consignment contained further material of the above).

(4) Two consignments of well-grown larvæ of *Eriocrania semipurpurella*, in spirit.

(5) Three consignments of first instar larvæ of *Micropteryx calthella*, fixed in Carls' Fixative, as requested by me.

(6) Two consignments of female imagines of *Micropteryx calthella*, similarly fixed in Carls' Fixative.

(7) Two consignments of cocoons of *Eriocrania semipurpurella*, freshly dug up, and containing living larvæ when posted.

Besides the material sent by Dr. Chapman, I have received specimens from the following correspondents, to all of whom I now offer my best thanks for their generous help.

From Mr. Edward Meyrick, F.R.S., set specimens of the following genera:—*Sabatinca* (two species), *Micropteryx* (three species), *Mnemonica* (two species), *Eriocrania* (one species), and *Mnesarchæa* (two species); in all, five genera, ten species, and twenty-two specimens.

From Mr. Alfred Philpott, Invercargill, N.Z., set specimens of the genera *Sabatinca* (four species), and *Mnesarchæa* (two species), of which three species, *S. caustica* Meyr., *S. barbarica* Philpott, and *M. parucosma* Meyr., were not included in Mr. Meyrick's consignment. Also a single larva of *Sabatinca* sp.

From Mr. K. J. Morton, of Edinburgh, numerous examples of *Micropteryx aruncella* Scop., in alcohol.

From the Museum of Comparative Zoology, Cambridge, Mass., by exchange, through Mr. Preston Clark, of Boston, Mass., two larvæ, a pupa and a set imago of *Mnemonica auricyanea* Wals.

From Dr. A. J. Turner, of Brisbane, set specimens of *Sabatinca calliplaca* Meyr., the only known Australian representative of the family.

Thus the material upon which this paper is based consists of representatives of five genera and fourteen species, together with the larval forms of four genera and pupæ of two. The genera *Epinartyria* (two species from N. America), *Micropardalis* (one species from New Zealand), and *Neopseustis* (one species from India) remain unknown to me except through the published descriptions. No larval or pupal forms appear to be known of genera other than those received for this work.

Classification.

For the purpose of this work, it will not be necessary to go back beyond Meyrick's classification in "Genera Insectorum" (6),

which is here accepted provisionally, as already explained. A short outline of this classification is here given:—

Subfamily MNESARCHÆINÆ.

No mandibles. Tongue short. Labial palpi well-developed. Middle tibiæ with two apical spurs.

Mnesarchæa Meyr., type *paracosma* Meyr. N.Z., three species.

Subfamily ERIOCRANIINÆ.

No mandibles. Tongue short. Labial palpi well-developed. Middle tibiæ with one apical spur.

Neopsenstis Meyr., type *calliglauca* Meyr. India, one species.

Eriocrania Zeller, type *semipurpurella* Steph. Europe, nine species.

Muemonica Meyr., type *subpurpurella* Haw. Holarctic, eight species.

Subfamily MICROPTERYGINÆ.

Mandibles developed. No tongue. Labial palpi rudimentary or obsolete. Middle tibiæ with apical group of bristles, without spurs.

Epimartyria Wals., type *pardella* Wals. N. America, two species.

Micropteryx Hubn., type *aruncella* Scop. Palæarctic, twenty-seven species. (= *Eriocephala* Curtis, type *calthella* Linn.).

Micropardalis Meyr., type *doroxena* Meyr. New Zealand, one species.

Sabatinca Walker, type *incongruella* Walker. New Zealand, five species; Queensland, one species. (= *Palæomicra* Meyr., type *chrysargyra* Meyr.).

A new genus, *Anomoses*, has been recently added by Dr. A. J. Turner(11), based on a single new species from Queensland. This insect is, however, so different from the rest of the *Micropterygide* that I doubt whether it really belongs here. I think it should be placed in the family *Prototheoridae*, hitherto only known from South Africa.

The literature of the family is somewhat involved, owing to the continued inversion of the two names *Eriocrania* and *Micropteryx*. This was due to the adoption of the name *Eriocephala*

Curtis, for the genus *Micropteryx*, by a considerable number of authors, amongst whom we may mention Packard, Chapman, and Meyrick in their earlier works, as well as Sharp in the "Cambridge Natural History," following these. The name *Micropteryx* was then applied wrongly to *Eriocrania*, by those who used *Eriocephala* for *Micropteryx* itself. One has, therefore, always to bear in mind, that, in works where the names *Eriocephala* and *Micropteryx* are used to contrast these two very distinct generic types, *Eriocephala* should be correctly *Micropteryx*, and *Micropteryx* correctly *Eriocrania*.

The subdivision of the family *Micropterygidae* into two separate families, *Eriocephalidae* and *Micropterygidae*, corresponding with the two subfamilies *Micropteryginae* and *Eriocraniinae* as defined by Meyrick, was first proposed by Chapman in 1894(1); this arrangement was followed by Sharp in 1909(8), though not by Meyrick in 1895(6). In this latter year, Packard(7) emphasised the primitive condition of the mouth-parts in *Micropteryx* (which he called *Eriocephala*) by his division of the Order Lepidoptera into two Suborders, Lepidoptera Laciniata (or Protolpidoptera), containing only *Micropteryx*, and Lepidoptera Haustellata, containing all the rest, including *Eriocrania* (which he calls *Micropteryx*). He further emphasises the difference between *Eriocrania* and the remainder of the Lepidoptera Haustellata, by dividing this Suborder into two series, of which the first, or Palaeolepidoptera, contains only the *Eriocraniidae*, while the second, or Neolepidoptera, contains all the rest.

In 1917, Chapman(2), as already stated, raised the genus *Micropteryx* to ordinal rank, with the title Zeugloptera, on the characters mentioned by Packard, together with the new character emphasised by him, that the female of this genus possesses only a single terminal genital opening in the tenth abdominal segment, whereas all other Lepidoptera possess only nine segments in the female, and have two genital openings, one in the eighth segment for pairing, and a terminal one for oviposition. He says:—"It remains difficult to suggest that *Micropteryx* has any lepidopterous character except the possession of scales. The neuration is also, perhaps, *prima facie*, lepidopterous; but both

this particular neuriation and the possession of scales are to be found in insects having no claim to be lepidopterous."

On the other hand, Comstock in 1918(3), in removing the whole of the *Micropterygidae* (sens. lat.) to the Trichoptera, as stated above, bases that removal wholly upon the characters of the wings. These characters are, "in the *fore wings*, the coalescence of veins Cu and 1st A* at the base of the wing; the Z-shaped course of vein Cu; the formation of a serial vein consisting of the base of the media, the posterior arculus, and the longitudinal part of vein Cu; the coalescence of the tips of the second anal vein and of two of the branches of the third anal vein; and the cross-vein between the first and second anal veins. In the *hind wings*, the coalescence of veins Cu and 1st A at the base of the wing; the Z-shaped course of the cubitus; the anastomosis of the first and second anal veins; the longitudinal direction of the cross-vein connecting the second anal vein and the first branch of the third anal vein; and the form of the branching of the third anal vein. In addition to these common venational features, the fibulæ of the two insects are identical in structure." He concludes:—"The possession of this remarkable series of common features of their wings by these representatives of the Phryganeina and Micropterygina, and which is found in no insect not belonging to one of these two groups, can be explained only by assuming that it indicates a community of descent of the two groups. This conclusion is confirmed by the results of Dr. T. A. Chapman's study of pupæ. For these reasons, the Micropterygina must be regarded as more closely allied to the Phryganeina than they are to any other group of insects; that is, they are obviously Trichopterous insects."

We see, then, that there are three conflicting views as to the nature of the *Micropterygidae*, which may be summarised as follows:—

(1) *The Micropterygidae are true Lepidoptera.* This is the original view held by all past generations of entomologists, and still championed by Meyrick.

* It must be remembered that Comstock's Cu is really Cu₁, his 1A is Cu₂, his 2A is 1A, and his anterior branch of 3A is 2A.

(2) *The Micropterygidae are terrestrial Trichoptera.* This is the new view formulated by Professor Comstock.

(3) *The genus Micropteryx belongs to a new Order Zengloptera. Eriocrania, on the other hand, is a true Lepidopteron.* This is Dr. T. A. Chapman's view.

It is the object of this paper to try to discover which of these three views is correct; or, if none of them be acceptable, to try to find a substitute for them. The decision to be made is of the very greatest importance, not only in determining the vexed question of the true position of these archaic insects, but also because it radically affects the definition of the Archetype of the Order Lepidoptera; and hence, our decision as to the origin of that Order as a whole.

The first part of this paper is confined to the study of the wings alone. The rest of the Morphology of the *Micropterygidae* will be dealt with in a series of succeeding Parts.

Part i.—THE WINGS OF THE MICROPTERYGIDÆ.

Section i.—THE WING-VENATION.

In his book on the Wings of Insects (3, pp.314-318) Professor Comstock deals with the venation of this group. No attempt has been made to study the pupal tracheation, probably because the necessary material was not available. But drawings are given of the tracheation as partially preserved in a pair of cleared and mounted wings of *Mnemonic* sp., which offered very striking results, and on which Professor Comstock's conclusions are chiefly based.

My request to Dr. Chapman for cocoons of *Eriocrania* containing living larvæ was made principally with the object of obtaining the living pupa and studying the tracheation of the wings. Dr. Chapman very kindly obtained for me the larvæ in the spring of this year, and fed them until they went into the ground to spin up. In the South of England, these larvæ, apparently, are full fed about Midsummer, and soon go into the ground, making their tiny oval cocoons of grains of sand spun together. In these they remain until the following February, when they pupate, emerging as imagines in the spring. Dr. Chapman dug up the first lot of cocoons, fifteen in number,

on Sept. 2nd, and a second larger consignment of sixty-one cocoons was dug up and posted on Sept. 18th. Owing to the unfortunate and very severe outbreak of pneumonic influenza in New Zealand, the vessels carrying these consignments were both quarantined at Auckland, where they underwent a thorough fumigation. On arrival at Sydney, they were again quarantined and fumigated. Finally the mails were released, and again fumigated by the Postal Department. Thus the length of the journey was increased by at least a fortnight; and the insects, besides having to stand the great heat of a voyage across the Equator, were subjected to three severe fumigations.

I must confess that I did not expect that, under such conditions, any of these insects would reach me alive. However, they were little affected by their adventures, the larvæ being normal, the pupæ mostly alive but very weak. Out of the seventy-six cocoons so far received, only four contained live larvæ, seventeen contained pupæ, five were destroyed by fungus, and all the rest, amounting to 66%, or about two-thirds of the entire total, were parasitised by at least two species of Chalcid wasps. Most of these latter were still in the larval stage; a few were subpupæ or pupæ, but all were equally lively, and quite unaffected by their long journey.

The effect of the higher temperature on the larvæ of *Eriocrania* is then very obvious, in that they pupated long before their normal time. Of the seventeen pupæ examined, three were dead and somewhat shrivelled, two were only recently turned, one was apparently about half-developed towards the imaginal stage, and no less than eleven were very fully developed, with their wing-sheaths jet black and shiny, and all the parts of the imago fully formed.

It will thus be seen that, out of seventy-six specimens sent, only two were in a state suitable for my purpose, while a third could be used with less certainty. All three of these were carefully dissected, and the results here given are based on the study of all three, which agreed with one another in every particular.

Both the opening of the cocoon and the dissection of the pupa are surprisingly simple matters, considering their small size.

The cocoons were opened with a dissecting needle, by scratching the sand away along a zone corresponding with that along which a boiled egg is usually opened at breakfast. The appearance of a shiny black inner envelope was a sign that the larva had been parasitised, this being the cocoon of the Chalcid. The *Eriocrania* pupæ were free inside the cocoon, and could easily be lifted out without damage, on the point of the needle. They were all very inert, and made no attempt to move. I therefore killed and dissected them straight away, and was pleased to find that the removal of their wings was a very simple operation. The wings are even less glued together than is the case with the Mecoptera and Planipennia, being only slightly joined at their apices. These were at once separable with a needle, while the bases were easily cut away from the thorax with a sharp dissecting-knife. The separate wings were then floated out on to a slide, and examined first of all without a cover-slip. At this stage, drawings were made with the camera-lucida.

The tracheation being so fine, a high power was required for the study of the basal specialisations. For this, it was necessary to let down a cover-slip upon the wings. This had to be done very carefully, for fear of disarranging the delicate tracheation; but in each case the operation proved successful; so that further drawings under a higher power, together with photomicrographs, could be taken.

The wings being different in certain important particulars, in spite of their homoneurous appearance in the imago, it is advisable to deal with each wing separately, and then to make a comparison between them.

The Forewing. (Plate iii., figs. 1-3; Text-figs. 1-2).

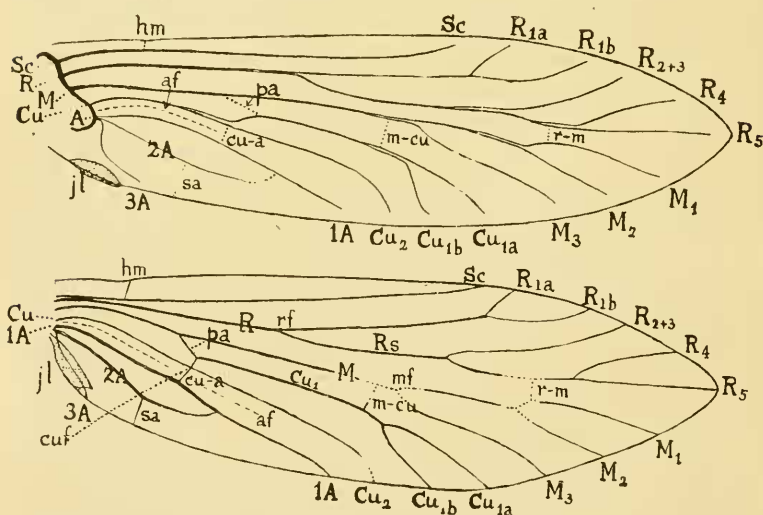
The tracheation of the forewing is of a very generalised type, as may be seen from Text-fig. 1. All the main tracheæ are quite distinct and separate from their bases outwards. The points to be noted are:—

(1) R_1 gives off a pterostigmatic veinlet R_{1a} , homologous with one of the corresponding veinlets in many Mecoptera, Megaloptera, Planipennia, and in a few Trichoptera.

(2) R_{2+3} is a simple, unbranched trachea. This is a constant character for the genus.

(3) The median fork is placed far distad, well beyond half-way along the wing.

(4) There is no sign of a separate trachea M_1 . In this, *Eriocrania* agrees with the great majority of Lepidoptera, both Homoneura and Heteroneura, but differs from the Trichoptera, in which all the more archaic genera have M_1 not only present, but quite separated from Cu_{1a} .



Text-fig. I.

Forewing of *Eriocrania scimpurpella* Steph. Above, the pupal tracheation, ($\times 54$); below, the imaginal venation, ($\times 18$). For lettering, see p. 136.

(5) *The Cubitus is definitely three-branched*, the first dichotomy into Cu_1 and Cu_2 taking place at about one-fourth of the wing length from the base; further distad, Cu_1 forks again into Cu_{1a} and Cu_{1b} .

This very important character is also to be found in the Megaloptera, where the comparison with *Eriocrania* is exact; in the Planipennia, where the branching of Cu_1 usually consists of a

series of descending branches arranged more or less pectinately; and probably also in the older Trichoptera, though the homologies in this Order are not yet quite clear, owing to the absence of the preceding tracheation in the pupal wing.

(6) The *anal furrow* (*af'*) is very definitely marked, and quite distinctly separates the cubitus from the first analis.

(7) There are three separate anal tracheæ present, none of them branched. Trachea 2A tends to bend towards 1A distally, but does not meet it. Trachea 3A is very short, and descends to the wing-border just beyond the distal end of the jugal lobe.

The above interpretation is so obvious that it can scarcely be questioned. Nevertheless, Professor Comstock, in his recent book already quoted (3), while figuring the tracheation, as far as he could make it out in the imago, as essentially the same as that here figured for the pupa, gives a different interpretation to the limits of the cubital and anal tracheæ. The reasons for this appear to be two:—

(1) Professor Comstock starts with the assumption that the cubitus was originally only two-branched. This assumption is applied to the Aquatic Trichoptera, where it appears to fit, and then the tracheation of the Micropterygina is interpreted along the same lines. In order to do this, it is asserted that trachea 1A has migrated forwards and become fused with Cu basally; but no proof is offered of such an astonishing specialisation, in so archaic a group as the *Micropterygidae*.

(2) In many Lepidoptera, the original dichotomy of Cu into Cu₁ and Cu₂ occurs very close to the base; and, as is usual in this Order, the tracheæ split back even further than the veins; so that, in the higher groups, the division of Cu may take place almost or quite on the alar trunk trachea. This lends support to the idea that there are here two main tracheæ, Cu and 1A. Against this, it may be mentioned that, firstly, the anal group of three tracheæ can always be made out, arising very far away from these other two; secondly, that, in many cases, especially in the older families, this splitting back does not reach as far as

the alar trunk; and, thirdly, that, in a number of families (*e.g.*, in the *Saturniidae* and some Butterflies*) the radius is likewise split back to the alar trunk, and may even arise as five separate tracheæ (*Antherea eucalypti*); yet nobody questions that these all belong to the radius.

If Professor Comstock's interpretation be correct, we are bound to ask, how is it that it is in the ancient *Micropterygidae* that this specialisation (*i.e.*, the fusion of Cu and 1A) reaches its highest expression; and how is it that, in the most highly specialised of all Lepidoptera, *viz.*, the *Saturniidae* and the Butterflies, we find a retrogression to what, on this view, must be the nearest approach to the primitive type, *viz.*, that in which Cu and 1A arose separately from the alar trunk? This question is unanswerable, except by the admission that it is the higher families of the Lepidoptera which show the greatest splitting back of the tracheæ, while the original condition is preserved more completely in the older families, and especially in the *Micropterygidae*. In other words, the cubitus is three-branched, and the true 1A is the first of the quite separate anal group of tracheæ, lying in its natural position, *posterior to the anal furrow*.†

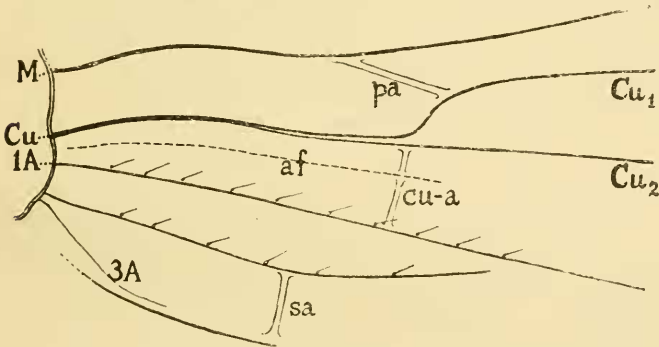
It should also be noted that there are already three separate anal tracheæ recognisable in the anal group, without the supposed 1A of Comstock's interpretation. If Comstock is right, then it is necessary to explain how the *Micropterygidae* (and most Lepidoptera) come to possess four anal veins, whereas the older Orders Mecoptera, Megaloptera, Planipennia, and Trichoptera are admitted to possess only three.

In Plate iii., fig.3 and Text-fig.2, the actual condition of the primary cubital fork in the pupa of *Eriocrania* is shown. It will be seen that the line of the main stem of Cu is continued beyond the fork, not by Cu₁, as we might have expected, but by Cu₂. From the fork itself, Cu₁ arches up at an angle to the main stem, and then turns to run parallel to and above Cu₂ until it again forks into Cu and Cu_{1b}. A pale band passing from M to

* Also sometimes in the ancient *Hepialidae*!

† The full proof of the limits of Cu in Lepidoptera will be given in Part iii. of the "Panorpid Complex."

Cu₁ a little distad from the fork indicates the position in the imago of the *posterior arculus*, which is destined to form part of the serial vein made up of the base of M, the posterior arculus, and the distal portion of Cu₁. A very careful examination of the tracheæ forming Cu in the pupal wing shows that the actual dichotomy of Cu into its two main branches lies slightly basad from the point which becomes the cubital fork in the imago, as shown in Text-fig.2. It will be seen that the same type of splitting back to a point before the actual bifurcation of the imaginal veins is also to be found in all the other dichotomies, not only in *Eriocrania*, but likewise in all Lepidoptera.



Text-fig.2.

Portion of basal tracheation of forewing of the pupa of *Eriocrania semipurpurella* Steph., to show the *cubital fork* (Cu dividing into Cu₁ and Cu₂), the *posterior arculus* (*pa*), the *anal furrow* (*af*), the *cubito-anal cross-vein* (*cu-a*), and the courses of the three anal veins, with the *sub-anal cross-vein* (*sa*). Note the splitting back of the cubital trachea basad from the true position of the cubital fork in the imago; also the macrotrichia developed along the courses of the future first and second anal veins; ($\times 132$).

Careful dissections of the pupal forewings of *Hepialidae* show that this family also possesses the same conditions in the region of Cu, the arching up of Cu₁ and the position of the posterior arculus being exactly the same as in *Eriocrania*. The differences between the two wing-types lie only in the more generalised shape of the Hepialid wing, the more basal position of the

dichotomies of R and M, and the somewhat greater reduction of the anal area. R_{1a} is, of course, absent in *Hepialidæ*, and R_{2+3} is always forked near the apex.

Text-fig.1 shows also the venation of the imaginal forewing of *Eriocrania*, for comparison with the pupal tracheation. It will be seen that the serial vein formed from M, *pa* and Cu_1 is by no means straight, as it is in some higher types, and there is little difficulty in recognising the parts that go to its composition. The only other specialisations are (a) the distal union of 2A with 1A to form the forked anal vein (note that trachea 2A does not meet 1A); and (b) a great weakening of portions of the imaginal venation, giving rise to three hyaline areas, within which the main veins and cross-veins alike are obliterated. These areas are known as *thyridia*, and are also to be found in Trichoptera, Mecoptera, and Planipennia. In Text-fig 1, I have indicated the courses of the veins on the thyridia by dotted lines; one of them covers the median fork, another runs from R_{4+5} to the dichotomy of M_{1+2} , and a third covers the distal end of Cu_2 . The only true cross-veins present in the forewing of *Eriocrania* are the humeral (*hm*), the radio-median (*r-m*), the medio-cubital (*m-cu*), the posterior arculus (*pa*), the cubito-anal (*cu-a*), and the subanal (*sa*). It should be noted that the basal piece of Cu_1 has frequently been mistaken for the cubito anal cross-vein, as by Forbes*(4), while the misapprehension as to the real identity of 1A has led to an incorrect naming of the true cubito-anal itself.

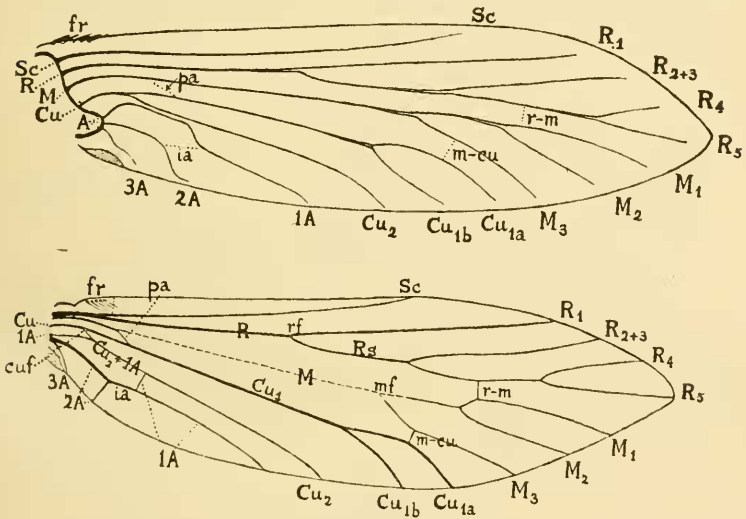
The Hind wing. (Plate iii., fig.1, Text-figs.3-4).

The tracheation of the hindwing of the pupa, though on the whole resembling that of the forewing, differs from it in at least two very important points. Firstly, the cubital fork lies much closer to the base of the wing; and, secondly, there is a very important specialisation in the course of 1A, this trachea coming to lie alongside Cu_2 for a considerable distance, as may be seen in Text-figs.3-4. Consequent upon the changed position of the cubital fork, the posterior arculus (*pa*) is shorter and much less

* The wing figured by Forbes is actually that of *Micropteryx* (*Eriocphala*) *thunbergella*.

conspicuous in the hindwing than in the fore; this is well seen by comparing Text-figs. 2 and 4.

The course of 1A is very tortuous, as may be seen from Text-figs.3-4. Arising with the other anal veins far from the base of Cu, it bends forward, and approaches Cu₂ just as the latter leaves the cubital fork. It runs alongside this latter vein for some distance, and then bends downwards again away from it, finally running subparallel to and below it to the wing-border. If,



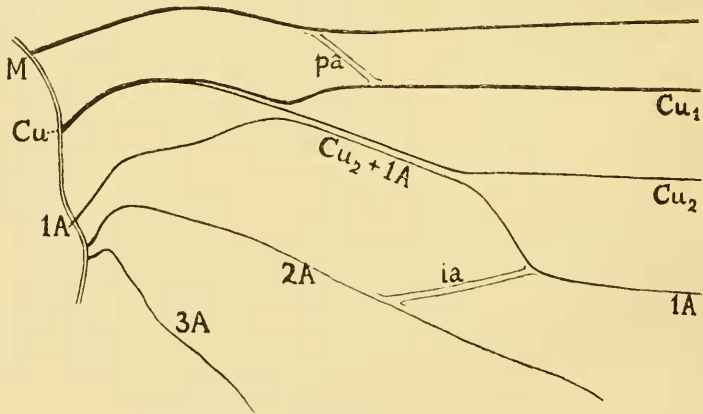
Text-fig.3.

Hindwing of *Eriocronia semipurpurella* Steph. Above, the pupal tracheation, ($\times 60$); below, the imaginal venation, ($\times 19$). For lettering, see p.136.

now, we turn to the imaginal venation, we see that the course of this vein is even more carefully concealed, since a single vein, Cu₂ + 1A, there occupies the portion where the two tracheæ ran alongside one another; in other words, a complete fusion of these two veins has taken place in this region. The part of 1A descending from Cu₂ distad from this fusion appears like a cross-vein, and has been so considered by some authors. The distal part of 1A forms, in the imago, the distal portion of a serial vein, of

which the basal part is formed from 2A, and the middle connecting piece by a longitudinally placed cross-vein, the inter-anal (*ia*). The distal end of 2A descends transversely to the wing-border, and thus resembles a cross-vein.

Thus we see that the cubital and anal portions of the fore- and hindwings in *Eriocrania* are really very different, though there is a superficial analogy between non-homologous parts; as, for instance, between the curved distal part of 2A in the forewing (where it joins up with 1A) and the inter-anal cross-vein of the hind; and again, between the sub-anal cross-vein of the forewing and the descending distal portion of 2A in the hind.



Text-fig. 4.

Portion of basal tracheation of hindwing of the pupa of *Eriocrania semipurpurella* Steph., to show the *cubital fork* (contrast its position with that of the forewing) and the tortuous course of trachea 1A, with the manner of formation of the fused vein $Cu_2 + 1A$. *ia*, inter-anal cross-vein; *pa*, posterior arculus; ($\times 165$).

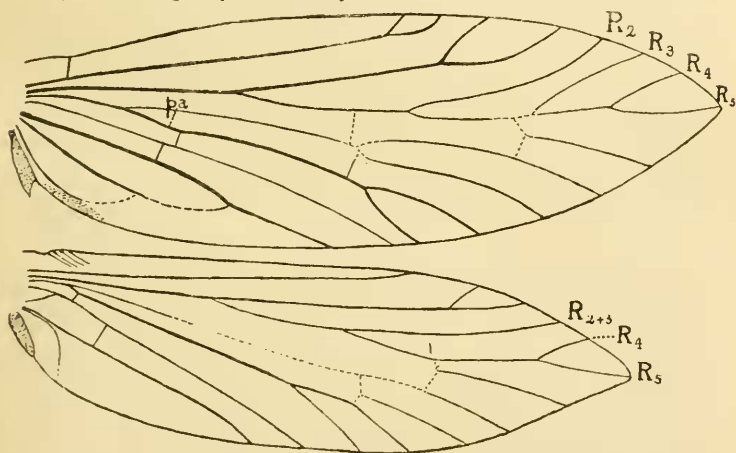
It should be noted that the subcostal vein is proportionately shorter in the hindwing than in the fore, ending only a little beyond half-way along the costal border. The costal space is proportionately narrower. The pterostigmatic region is longer and narrower, and not crossed by a vein R_{1a} . The radio-median cross-vein is plainly visible; whereas, in the forewing, it is lost in the thyridium. The imaginal venation of the hindwing is

much weaker than that of the fore; and most of the main stem of the media is obsolescent, from just distad of the posterior arculus to the median fork. The medio-cubital cross-vein is placed much more distad than in the forewing, descending from M_3 upon Cu_{1a} . Cu_2 is also a very weakly indicated vein. There are no true thyridia in the hindwing.

Other differences between the two wings, apart from that of size, are the obsolescence of the humeral cross-vein, the presence of the frenulum, and the reduction of the jugal lobe, in the hindwing.

Comparison with the Venation in other Genera.

The pupal tracheation is not available for the study of other genera of the *Micropterygidae*. This is, however, very little drawback, now that we have the pupal tracheation of *Eriocrania*; for we shall be able to show that the same type of venation holds throughout the group, with only minor differences of detail.



Text-fig. 5.

Wings of *Mnemonica subpurpurella* Haw., ($\times 19$). pa , posterior arculus.

The genus that is most nearly allied to *Eriocrania* is *Mnemonica* (Text-fig. 5), which was separated out from the older genus *Eriocrania* by Meyrick in 1912, its type (*subpurpurella* Haworth)

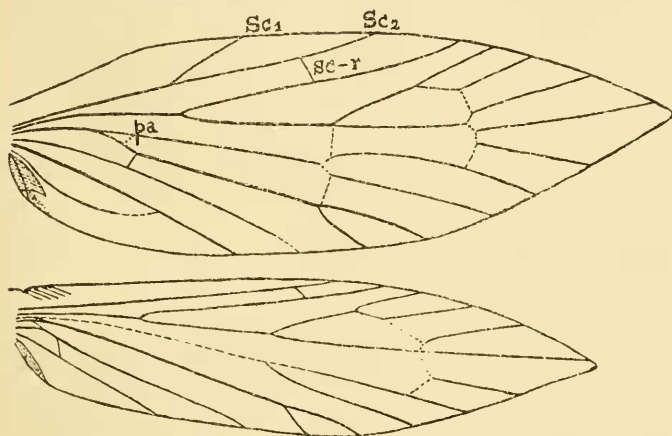
having been placed originally in *Micropteryx*, and removed to *Eriocrania* when that genus was formed later on. *Mnemonic*a differs from *Eriocrania* in having R_2 and R_3 existing as separate veins in the forewing. I have marked these veins in Text-fig.5. It will be seen that, in this genus, R_s is not dichotomously branched, but that R_3 arises from what we usually regard as the common stem of R_4 and R_5 . All specimens examined by me show this condition, which is also the one figured by Meyrick (6. p.802), as well as by Comstock (3, p.314). I fail, therefore, to understand the remark of the latter author on the same page that "this is an exceptional feature; usually the forking of the radius is dichotomous."* From an examination of all the specimens in my possession, representing sixteen wings belonging to three species of this genus, all of which agree in this character, I have very little doubt that the condition figured is the more usual one for the genus.

Further differences between *Eriocrania* and *Mnemonic*a are the presence of an extra distal branch of Sc in the forewing of the latter, and the distal forking of R_1 in the hindwing as well as the fore. There is also the complete joining-up of the distal end of $3A$ on to $2A$ in the forewing, apparently brought about by a union of $3A$ with the cross-vein sa , and the more primitive condition of vein $2A$ in the hindwing. Both these characters, however, appear to be subject to some variation in individual specimens.

It will thus be seen that the differences between *Mnemonic*a and *Eriocrania* are most certainly of no higher than generic value (as regards the wing-venation), and that there is nothing to prevent us naming all the parts of the venation of *Mnemonic*a with certainty, now that we know the tracheation of the wings of *Eriocrania*. The peculiar differences in the course of the cubitus and anal veins in fore- and hindwings can all be made out easily in *Mnemonic*a, simply by comparing the venation with that of *Eriocrania*.

* So also the forking of R_{2+3} far distad in the hindwing, figured by Comstock, would appear to be aberrant, since Meyrick states that "vein 10 is absent" in hindwing, and my specimens agree with this.

Turning next to the older genus *Micropteryx* (Text-fig. 6), representing a different subfamily from that in which *Eriocrania* and



Text-fig. 6.

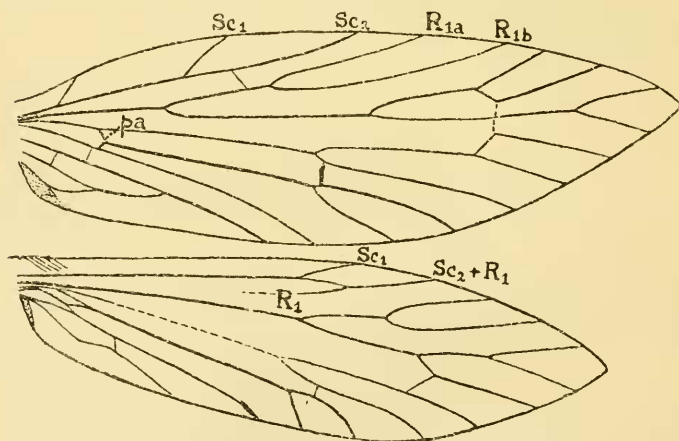
Wings of *Micropteryx aruncella* Scop. ($\times 27$). *pa*, posterior arculus; *sc-r*, cross-vein from Sc to R_1 ; Sc_1 , oblique branch of Sc crossing enlarged costal area of forewing.

Mnemonic are placed, we again find a closely similar type of venation present. The radial sector is, however, dichotomously branched in both wings, and possesses the full number of branches (four). R_1 is unbranched; but a strong branch (Sc_1) is developed, in the forewing only, from the middle of Sc , running obliquely across an enlarged costal area. A cross-vein (*sc-r*) is developed distally between Sc and R_1 in both wings, but the humeral cross-vein is absent. The posterior arculus (*pa*) is very prominently shown in the forewing, but is almost obliterated in the hind, the cubital fork being placed exceedingly close to the base of the wing. Vein 3A does not loop up with 2A in the forewing, but remains primitive, the cross-vein *sa* being apparently absent.

The wings of *Micropteryx* are more sharply pointed than those of the *Eriocraniine*, and show more markedly that secondary tendency towards a symmetrical shape, about a median longitudinal axis, which is more or less characteristic of the whole family. This I regard as a specialisation, probably due to the

manner of flight, and strictly comparable with the similar specialisation to be seen in the wings of the *Psychodidæ* amongst the Diptera. The broadened costal area of *Micropteryx*, with the oblique branch developed from Sc, is to be regarded as correlated with this specialisation rather than as an archaic feature of the wing; it should be noted that both are absent from the narrower hindwing.

There is, then, no difficulty in recognising the same type of venation in *Micropteryx* and in *Eriocrania*; though, if we did not possess the tracheation of the latter to guide us, we might indeed find it difficult to recognise the true courses of the cubitus and anal veins in the hindwing of this genus.

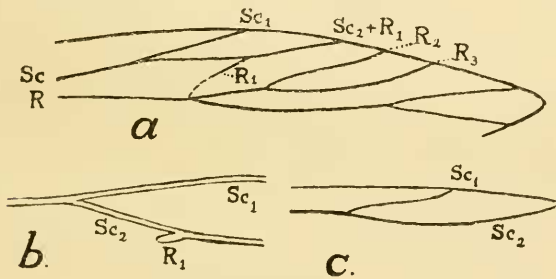


Text-fig.7.

Wings of *Sabatinca incongruella* Walk. ($\times 18$). *pa*, posterior areculus; R_1 , in hindwing, the obsolescent portion of the main vein R_1 ; $Sc_2 + R_1$, in hindwing, the fused distal ends of Sc and R_1 ; Sc_1 , oblique branch of Sc crossing enlarged costal area of forewing.

Passing from *Micropteryx* to the closely allied *Sabatinca* (Text-fig.7), we find a very similar type of wing, both in shape and venation. The costal area of the forewing is enlarged, as in *Micropteryx*, and carries not only the extra branch from Sc, but also the archaic humeral cross-vein. A remarkable feature of this wing is the strong distal fork of R_1 , comparable with that

of *Mnemonicæ*, but larger, and not occurring in the hindwing. This is properly regarded by Meyrick as a primitive character, since R_1 was certainly originally a branched vein. In the same region of the hindwing, however, we meet with a very remarkable specialisation, viz., the capture of R_1 , not far from its distal end, by Sc_2 . As a consequence of this, R_1 tends to shorten, and finally to become aborted basad from this point. In the type species of the genus, *S. incongruella* Walk., the basal portion of R_1 is already obliterated, and the rest of the vein appears as a short "returning" or "recurrent" vein attached to Sc_2 , as shown in Text-fig.7. I find this condition in all my specimens of this species, and also in *S. barbarica* Philpott. In *S. caustica* Meyr., the recurrent portion of R_1 is reduced to a small stump, about the size of a scale from the same wing, as shown in Text-fig.8, *b*. In *S. calliplaca* Meyr., the only known Australian species, even this stump is absent, and there is no sign at all of the presence



Text-fig.8.

- a*. Portion of venation of hindwing of *Sabatinca chrysargyrea* Meyr. ($\times 25$) to show the complete R_1 . *b*. Portion of venation of hindwing of *S. caustica* Meyr., to show small remnant of R_1 attached to Sc_2 , ($\times 60$). *c*. Portion of venation of hindwing of *S. calliplaca* Meyr., with R_1 entirely eliminated, ($\times 25$).

of R_1 (Text-fig.8, *c*). On the other hand, in both my specimens of *S. chrysargyrea* Meyr., R_1 is still complete, though very weakly formed basally. One specimen shows R_1 arising exactly from the forking of R_s into R_{2+3} and R_{4+5} (Text-fig.8, *a*), while the second shows it arising somewhat further distad along R_{2+3} . Both conditions are, of course, specialisations from the original

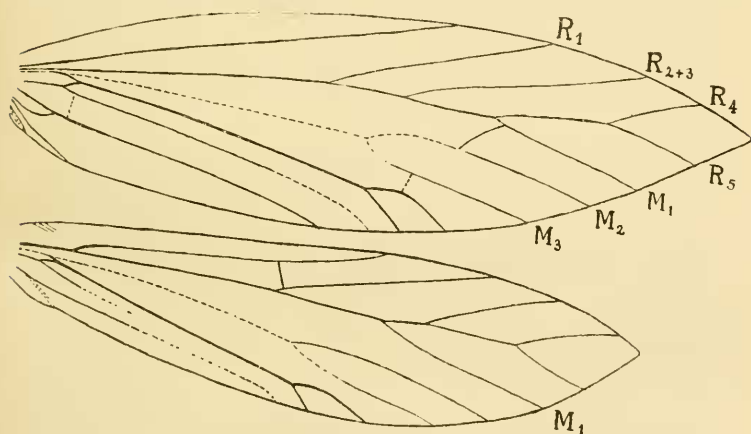
position; and hence we may say that R_1 , though very variable in the hindwing of this genus, is always more or less specialised in its formation.

Meyrick figures the hindwings of both *S. chrysargyra* and *S. incongruella* with a complete and normally placed R_1 , and omits Sc_2 from the hindwing of the former species (6, Plate, figs. 11, 12). If these figures are correct, then the variability in the structure of R_1 in the hindwing of *Sabatinca* must be very great. I have, however, mounted and studied a considerable number of hindwings of this genus, and in none of them have I seen anything comparable with what Meyrick figures.

Reviewing the above evidence, we see that the four genera *Sabatinca*, *Micropteryx*, *Mnemonica*, and *Eriocrania* are closely allied as regards their wing-venation. *Sabatinca* is perhaps the most archaic, but cannot be the direct ancestor of *Micropteryx*, on account of the specialisation of R_1 in the hindwing. Both *Sabatinca* and *Micropteryx*, again, are more specialised than the other two on account of their more symmetrical, sharply-pointed wings; and hence they can neither of them be the direct ancestor of the *Eriocraniine*. *Mnemonica* is older than *Sabatinca*, not only in the shape of its wings, but also in having R_1 forked in both wings; but it has mostly lost the original dichotomic arrangement of the branches of R_s —a very important specialisation—and has one branch of R_s absent from the hindwing. *Eriocrania* may well be a direct derivative from *Mnemonica*, by loss of one branch of R_s in the forewing also.

The remaining genus, *Mnesarchea*, (Text-fig. 9) presents a remarkable venational problem. In both wings, one vein has been lost; and a careful examination of the courses of the remaining veins, in the two species *M. paracosma* Meyr., and *M. hama-delpha* Meyr., shows us at once that this vein is the same as the one lost in *Eriocrania*; in other words, R_{2+3} is an unbranched vein in this genus. In my specimens of the type species *paracosma*, the vein M_3 is quite clearly to be seen, still attached to M_2 by a definite stalk, as well as to R_5 by the cross-vein *r-m*. Meyrick, however, figures the forewing of this species with M_1 directly attached to R_{2+3} , and with no attachment at all to M_2 .

Further, he states that the missing vein is No. 11, *i.e.*, R_1 . This is obviously wrong, as may be seen at once from Meyrick's own figure, and the one here given of the allied species *M. hamadelpha*. Other specialisations are: the great reduction in the size of the jugal lobe and the frenulum (in some specimens, it is not at all easy to see that either of them exists); the position of the cubital fork very close to the base in both wings, and the consequent reduction in the size of the posterior arculus; the great reduction in 2A in the forewings, so that it loops up with 1A very close to the base; and the reduction of Cu_2 and the anal veins through the narrowing of the base of the hindwing.



Text-fig. 9.

Wings of *Mnesarchaea hamadelpha* Meyr. ($\times 20$). Note M_1 entirely captured by R_5 in the hindwing.

In *M. hamadelpha* Meyr., (Text-fig. 9) there is a further specialisation (at least, in the two specimens examined by me) in that R_5 has completely captured M_1 in the hindwing, the original connection with M_2 being completely lost. As this is exactly similar to the condition shown by Meyrick for the *forewing* of *M. paracosma*, it is possible that this particular specialisation occurs fairly frequently in either wing of either species, when a sufficient number of individuals is examined.

From the above remarks, it will be seen at once that *Mnesar-*

chea might well be a direct derivative from *Eriocrania*, considerably more specialised, and, therefore, rightly placed in a separate subfamily. In the next section, it will be seen how very different the scales of this genus are from those of all the rest of the *Micropterygide*. If, therefore, it should turn out that the life-history of this genus, when discovered, is very distinct from that of both *Eriocrania* and *Micropteryx*, there would then be a strong case for its separation out as a distinct family *Mnesarchæide*, characterised by the combination of the loss of the forking of R_{2+3} , together with the remarkable specialisation in the structure of the scales. As these latter are of the greatest importance in considering the claim of the *Micropterygide* to be included in the Lepidoptera, I shall deal with them fully before comparing the wings of this family as a whole with those of Lepidoptera and of other Orders.

Section ii. THE SCALES.

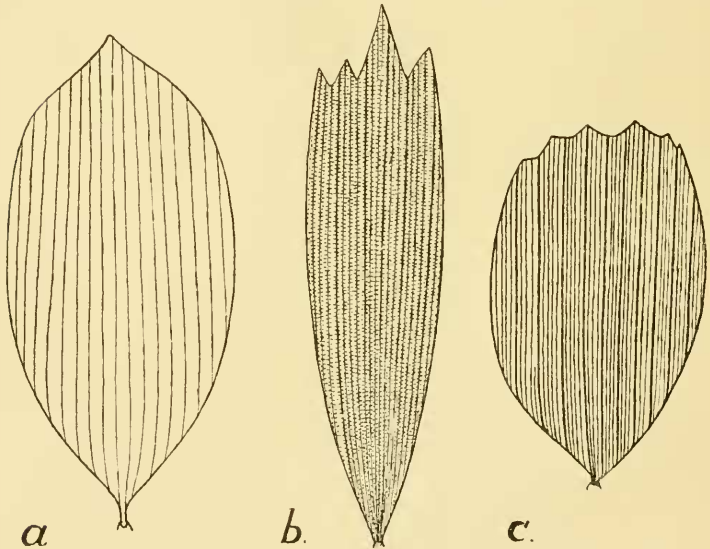
In all the *Micropterygide*, both microtrichia and macrotrichia are present, as in all the more archaic members of the Orders Megaloptera, Planipennia, Mecoptera, Diptera, Trichoptera, and Lepidoptera. The presence of microtrichia in itself is, therefore, no argument in favour of the inclusion of this family in any one of these Orders, in preference to any other. But the fact that they are of exceptionally small size, as they are in all Lepidoptera that possess them, must speak for the Lepidopterous nature of the family. In the same way, the presence of macrotrichia in itself is no argument in favour of any one of the six Orders as against another; but the fact that most of them are highly specialised as *scales* is of the greatest importance.

Various authors have depreciated the value of the presence of scales in this respect, by remarking that scales also occur in the Trichoptera and Diptera. They forget to add, however, two very important facts; firstly, that scales only occur in a few specialised representatives of these two Orders, and are certainly not to be found in the most archaic groups of either Order; and, secondly, that, in the Trichoptera at any rate, the scales are of a much more primitive type, even in the highest genera. Leaving

out of account the supposedly androconia-like bulbous macrotrichia of the males of one particular, highly-specialised genus (*Enoicylu*), which clearly do not enter into the question, the only scales known in the Trichoptera are very narrow, elongate, lanceolate scales, with not more than four or five longitudinal striæ at the most. These are confined to a few isolated genera in the families *Sericostomatide* and *Leptoceridae*, but are never found in any representatives of the *Rhyacophilide* or *Hydropsychide*, which are rightly regarded as the most archaic families of the Order. Nobody could possibly point to any connection between the *Micropterygide* and the Trichoptera, except through the *Rhyacophilide*, in which the venational similarity between fore- and hindwings is still to a great extent preserved. Hence the fact that broad, well-developed scales are to be found on all *Micropterygide* is strong evidence in favour of their being true Lepidoptera, since this Order is *the only one known in which scales occur universally from the lowest to the highest members of the Order*.

Let us then examine the types of scales to be found within the *Micropterygide*. Text-fig. 10, *a* shows a greatly magnified, broad scale from the wing of *Sabatinca incongruella*. (As in all Lepidoptera, the macrotrichia in this genus show all stages from a simple hair, through a flattened hair and various grades of narrow to moderately wide scales, to broad scales; the latter being the most highly developed, we shall study these only). The principal characteristics of this scale are: - its transparency, due to absence of internal pigment; its regular shape, without any scalloping of the distal border; the uniform delicacy of the parallel longitudinal striæ; and the absence of any sign of cross-striolation. This combination of characters marks off this type of scale very distinctly from any other known in the whole of the Lepidoptera (excluding *Micropterygide*). A careful examination of the scales to be found in the genera *Micropteryx*, *Mnemonic*, and *Eriocrania* shows us that they all possess broad scales very closely similar in type to those of *Sabatinca*. The most generalised of all would appear to be those of *Mnemonic* (Text-fig. 11, *c*), from which it is easy to derive the broader and

somewhat distally flattened scales of *Eriocrania* (Text-fig.11, *d*) on the one hand, and the slightly pointed scales of *Sabatinea* (Text-fig.11, *b*) on the other. From this latter form, by a considerable shortening, and a further specialisation in the form of the distal portion, we arrive at the form seen in *Micropteryx* (Text-fig.11, *a*) Thus all four genera agree very closely in the



Text-fig.10.

Scales of *Micropterygidae* ($\times 600$). *a*, broad scale from wing of *Sabatinea incongruella* Walk.; *b*, medium width scale, and *c*, broad scale from wing of *Mnesarchaea hamadelpha* Meyr., (cross-striolation somewhat emphasised in *b*, but omitted in *c*, being too delicate for reproduction).

form of their broad scales. Further, as this type of scale is very distinct from any other known in either of the Orders Trichoptera or Lepidoptera, it is clear that the affinity of these four genera is placed beyond serious doubt by the possession of this character in common.

Turning next to the genus *Mnesarchaea*, I have figured both a broad scale (Text-fig.10, *c*) and one of medium width (Text-fig. 10, *b*), since both afford comparisons with scales from other

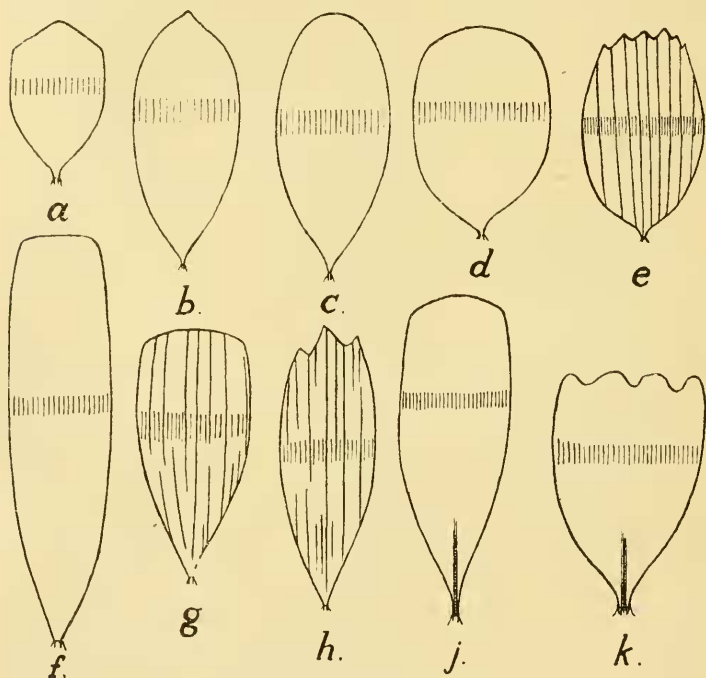
families of Lepidoptera. Both these scales are remarkable for the following series of characters: – the scalloping of the distal border; the large number and consequent closeness of the parallel longitudinal striæ; the presence of a number of thickened or coarsened striæ; the presence of cross-striolation; and its attendant character, the presence of pigment granules in the scale itself. It should be further noted that the membrane of the wing in *Mnesarchæa* is quite transparent, while that of the other *Micropterygidae* always has more or less brown pigment deposited within it. Thus the beautiful metallic effects found in this family are due to the combination of pigment in the membrane with striation of the scales; but in the non-metallic *Mnesarchæa* the whole colour-producing apparatus is located in the scales.

We have now to enquire whether the scales of *Mnesarchæa* show any close resemblance to those of any known family of Lepidoptera. In Text-fig. 11, *h*, I give a drawing of the hitherto undescribed scales of *Prototheora* (Suborder Homoneura, family *Prototheoridae*), which will be seen to be exactly comparable with the medium-width scale from *Mnesarchæa* figured in Text-fig. 10, *b*. The only difference between the scales in this family and in *Mnesarchæa* is that the type of scale shown in Text-fig. 11, *h*, is the *broadest* to be found in the *Prototheoridae*, and it is interspersed with a number of scales that are not scalloped at the distal end, but merely lanceolate, or even oval. Cross-striolation is present in all the scales of this family, and, indeed, in those of every family of Lepidoptera, as far as I know, except only in the four genera of *Micropterygidae* already mentioned.

Two types of scale from the family *Hepialidae* are shown in Text-fig. 11, *f*, *g*, the first from *Charayia*, the second from *Perissectis*. Kellogg (5) supposed that the presence of coarsened striæ was peculiar to this family, since it had not been found in any other. We now see that this type of striæ is to be found in all three families of the Homoneura, but not in any known Heteroneura. The scales of *Hepialidae* appear to be distinguished by their flattened distal borders, as contrasted with the scalloped border of the scales of *Mnesarchæa* and *Prototheora*, and the

rounded or slightly pointed distal border found in the other *Micropterygidae*, and also in *Prototheora*.

Text-fig. 11, *j, k*, shows two types of scale from *Cebysa conflictella* Walk., an archaic Heteroneurous Lepidopteron usually placed



Text-fig. 11.

Different types of Lepidopterous scales ($\times 330$). *a*, from *Micropteryx*; *b*, from *Sabatinea*; *c*, from *Mnemonea*; *d*, from *Eriocrania*; *e*, from *Mnesarchaea*; *f*, from *Charaxia* (*Hepialidae*); *g*, from *Perissectis* (*Hepialidae*); *h*, from *Prototheora* (*Prototheoridae*); *j, k*, from *Cebysa* (*Plutellidae*). In all figures, the normal delicate striation is not completely filled in, but only indicated by the short parallel lines; the coarsened striae, when present, are indicated in full; and the cross-striolation, which is present in all except *a-d*, is entirely omitted, being too delicate to be properly visible at the given magnification.

in the *Plutellidae*. These are figured for comparison with *Mnesarchaea*, which Meyrick considers not far removed from the

Plutellidæ in the venation of its forewing. Like those of all other Heteroneura, these scales are devoid of coarsened striæ; but they show a kind of thickened stalk basally, such as may also be found in the *Oecophoridæ* and other families. The longitudinal striæ are very numerous and close together, and the cross-striolation very marked. The scales of most Heteroneura are scalloped or deeply angulated along the distal margin; a marked exception to this rule is the archaic family *Cossidæ*, in which scalloping is never found.

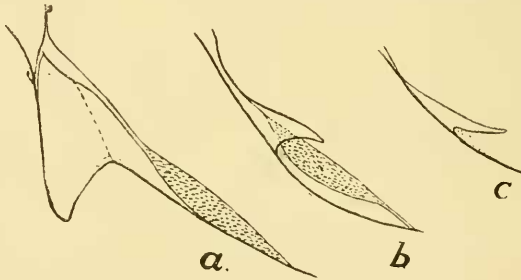
Section iii. THE WING-COUPLING APPARATUS.

In Part i. of my paper on the Panorpid Complex (9, p.298, Text-fig.10; Plate xxix., figs.1-3) I dealt with the wing-coupling apparatus of the *Micropterygidae*, and showed that it was of a jugo-frenate type, there being both a jugal lobe on the forewing and a distinct frenulum on the hind.

The conclusions arrived at in that paper were based for the most part on the study of New Zealand material, consisting of species of the genera *Sabatınca* and *Mnesarchæa*, and also on a long series of *Micropteryx aruncella* from Scotland. Of *Mnemonicæ*, I had at the time only three specimens, and of *Eriocrania* two, all received from Mr. Meyrick. Of these, only one specimen of each genus was sacrificed for the making of microscopic preparations, the others being kept intact.

In studying these preparations, I noticed that, of all the slides prepared by me, that of *Mnemonicæ* appeared to be the only one in which the jugal lobe was not doubled under the wing. As I had made a special effort to get this lobe spread out on the slide, I did not at the time attach much importance to this observation; particularly as, in the mounted wings of *Eriocrania*, I found the jugal lobe to be partly folded. However, on receipt of Professor Comstock's recent work (3, pp.314-6), it was at once evident to me that the jugal lobe of the *Eriocraniine* was quite different from that of *Sabatınca* and *Micropteryx*. Hence I made a further study of the whole of my material, with the result that I am now convinced that there are two very distinct types of jugal lobe to be found within the *Micropterygidae*.

In text-fig.12, I show these two types. The jugal lobe of *Sabatinca* and of *Micropteryx* is, as I have already described it, small, bent under the wing in a unique position, and able to engage the bristles of the frenulum, for which it acts as a primitive retinaculum (Text-fig.12, *b*). Further, there is an extensive patch of short, stiff spines, a specialisation from the macrotrichia of vein 3A, arranged in such a position as to aid in the retention of the frenulum. These were not figured in my former paper.



Text-fig.12.

Jugal lobes of *Micropterygidae*; *a*, from *Mnemonica subpurpurella* Haw., with elongated patch of short, stiff spines placed well distad from it; *b*, from *Sabatinca incongruella* Walk., with patch of similar spines placed just distad from it; *c*, from *Mnesarchea hamadelpa* Meyr., without any spiniferous area. (Drawn from cleared mounts, viewed from beneath, all three equally enlarged, $\times 54$).

In *Mnemonica* and *Eriocrania* (Text-fig.12, *a*), the jugal lobe is much larger, and does not pass under the forewing, but projects from it in the same manner as in *Rhyacophila*. It passes above the costal portion of the hindwing (in the position of flight), and thus helps in the coupling of the two wings. Beyond the jugal lobe, upon the distal part of vein 3A, there is developed an area of short, stiff spines, which probably also help in coupling the wings, by catching the bristles of the frenulum, though my material is not sufficient to decide this point for certain.

In *Mnesarchæa* (Text-fig.12, *c*), the jugal lobe is very weakly formed, but is of the same type as in *Sabatinca* and *Micropteryx*. There is no area of short, stiff spines, and the frenulum is also very weakly formed.

It is thus very evident that a single type of wing-coupling apparatus characterises the *Micropteryginae* and *Mnesarcheinae*, the latter being, as regards this character, an asthenogenetic offshoot from the former. The *Eriocraniinae*, on the other hand, have a jugal lobe resembling that of *Rhyacophila*. Thus we are placed in somewhat of a dilemma; since, on the characters of the wing-venation and mouth-parts, *Mnesarcha* would appear to be an offshoot of the *Eriocraniinae*; while the latter, judged by these same characters, are not so archaic as the *Micropteryginae* and hence should be further removed from *Rhyacophila*, if a Trichopterous origin for the family is to be maintained.

Section iv. DISCUSSION OF THE RESULTS.

We have now to consider the bearing of the results of our study of the wings of the *Micropterygidae* upon the systematic position of the group. We may best do this by asking the following questions in order, and answering them from the evidence now available:—

(1) *Are the Micropterygidae, or any part of them, rightly to be considered as forming a separate Order Zeugloptera?*

Dr. Chapman's new Order Zeugloptera includes only the genus *Micropteryx*. But it will be evident that, if it is to stand at all, it must also include the genera *Sabatinea* and *Micropardalis*; since these are so closely allied to *Micropteryx*, that any attempt to distribute the subfamily *Micropteryginae* between two separate Orders could not be countenanced for a single moment.

I take it, then, that Dr. Chapman would hold that the *Micropteryginae* form the Order Zeugloptera, while the *Eriocraniinae* and *Mnesarcheinae* are to remain within the Lepidoptera.

As far as the characters considered in this Part are concerned, it may be said at once that there is not a single one of them that is not to be found already in some Order other than Zeugloptera. The venational scheme is common to the Trichoptera and Lepidoptera; and some of its specialisations, notably the fusion of 1A with Cu_2 for some distance in the hindwing, are also to be found in many genera of the Mecoptera and Planipennia. The jugo-frenate type of wing-coupling is to be found in archaic

genera of the Orders Mecoptera and Planipennia. The scales of the *Micropteryginæ* and *Eriocraniinæ* are of similar structure, though those of *Mnesarchæa* are more highly specialised.

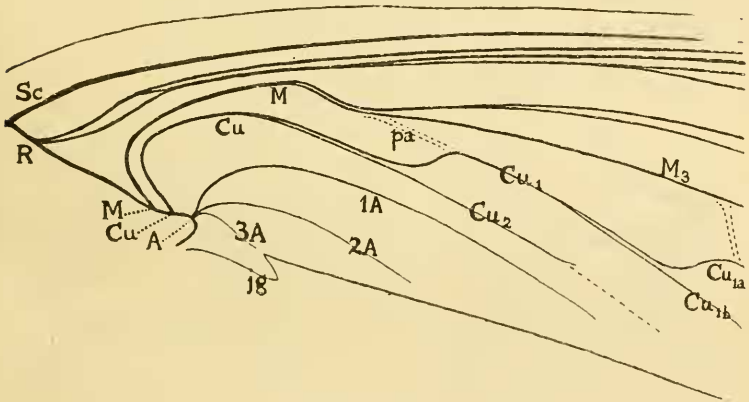
We can only conclude from this that, *on the characters considered in this Part*, there is no justification whatever for removing the *Micropteryginæ* to a separate Order Zeugloptera.

(2) *Are the Micropterygidae terrestrial Trichoptera?*

Professor Comstock relies almost entirely upon the venational scheme and the form of the jugal lobe (which he calls the *fibula*) for the justification of his removal of this group to the Order Trichoptera.

The complete discussion of the relationship between the wing-venational schemes of the Trichoptera and Lepidoptera has been selected by me as a necessary portion of the argument of the paper on the Panorpid Complex, Part iii., which, I trust, will be available in print at the same time as this paper. Hence there is no need for me to go into the same details here, but simply to refer the reader to that paper. The results, however, may be given here, with just two illustrations that will carry conviction. *There can be no doubt that the venational schemes of the Trichoptera and Lepidoptera are identical in all essential particulars.* In Text-fig.13, I give the tracheation of the base of the pupal forewing in the Hepialid *Charagia eximia* Scott. If this be compared with the tracheation of the forewing of the pupa of *Eriocrania* (Text-figs.1, 2), it will be seen at once that there is no difference of importance. *Charagia* is the more specialised, in that trachea Rs has been split back right to its very origin on the alar trunk, and the three anal veins are somewhat reduced. The variability in the condition of the anal venation in the forewings of Lepidoptera is very great, and in contrast with the specialised and very constant condition found in the forewings of all Trichoptera, in which 2A loops up with 1A, and 3A with 2A. In Lepidoptera, exclusive of the *Micropterygidae*, 3A is either very reduced or absent, and does not loop up with 2A. But 2A is frequently found to be looped up with 1A, giving the so-called "forked anal vein." Now the *Micropterygidae* as a whole repeat on a smaller scale this variability,

as may be seen by studying the anal venation of the five genera here figured. The Trichoptera, on the other hand, are constant in this character, throughout an immense series of known forms. Thus we can only conclude that, on this character, the *Micropterygidae* agree more closely with the Lepidoptera than with the Trichoptera. As regards the other venational specialisations of the forewing, they are all shared equally in common with the *Hepialidae* and with the Trichoptera, and there is no reason why anyone should prefer to remove them to the Trichoptera rather than to the *Hepialidae*.



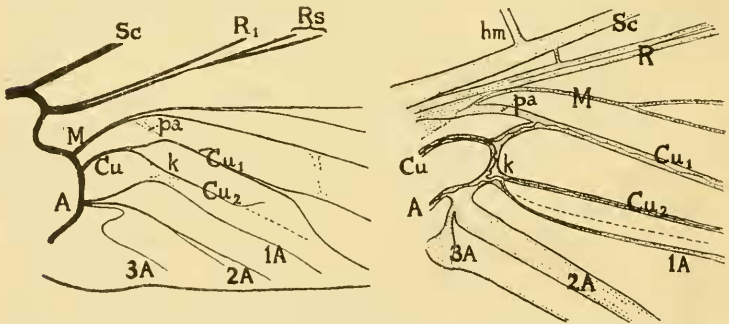
Text-fig.13.

Tracheation of forewing in pupa only two or three days old of *Charaxia erimia* Scott, drawn *in situ* after removal of the upper wing-sheath.

Note the splitting back of trachea R, and the two separate origins of Rs; ($\times 11$). For lettering, see p.136.

As regards the hindwing, there is the additional specialisation of the partial fusion of vein 1A with Cu_2 . In Text-fig.14, I show the condition of the tracheation of the pupal hindwing, near the base, in the genus *Leto* (*Hepialidae*), together with the corresponding imaginal venation. It will be seen that there is exactly the same condition, except only that the two tracheae Cu_2 and 1A do not lie so closely alongside one another. But the pupa studied was only a few days old, and the fusion may well become much closer towards the end of pupal life. It is

important to notice that, in the venation of *Leto*, the fusion of 1A with Cu_2 is actually accomplished for a short distance (Text-fig. 14, *k*), the basal piece of Cu_2 being bent transversely so as to look like a cross-vein. The reduction in the length of the fused portion in this family is surely to be expected, when we consider that the anal area has undergone reduction, through the narrowing of the base of the wing; the change in the direction of the anal veins from an inclination of about 30° to the longitudinal axis of the wing, in *Micropterygidae* and *Prototheoridae*, to more than 45° in *Leto* and other *Hepialidae*, and the comparative shortening of 1A, so that it ends up at less than one-fourth of the whole wing-length from the base in these insects, instead of at more than one-third as in *Micropterygidae*, must surely account for some slight alteration of this kind.



Text-fig. 14.

Hindwing of *Leto staceyi* Scott; to the left, the pupal tracheation; to the right, imaginal venation, basal part of wing only. *k*, in both figures, the point where fusion of veins Cu_2 and 1A takes place. As the tracheæ *Cu* and 1A were clearly visible in the fresh imaginal wing, they are drawn *in situ* in the right-hand figure. (Both figures $\times 4\frac{1}{2}$). For lettering, see p. 136.

Though it should be obvious that the presence or absence of a particular cross-vein ought not to be used as an ordinal character—since these structures, not being preceded by tracheæ, are exceedingly liable to variation—yet Professor Comstock includes in his ordinal diagnosis for the Trichoptera (inclusive of the *Micropterygidae*) the presence of the cross-vein between “the

first and second anal veins," *i.e.*, between 2A and 3A of our notation in this paper, and its *longitudinal direction* in the hindwing. Now, this cross-vein is present in some *Hepialidae*, as may be seen by referring to Comstock's own figures of *Pielus* and *Sthenopsis* (3, figs. 334, 335, 337); and, in the genera in which it is clearly visible in the hindwing (it is not to be seen in *Leto*, owing to the great swelling and fusion of 2A and 3A basally) it has an oblique position, not far removed from the longitudinal direction. Further, in many Trichoptera, as, for instance, in the *Hydropsychidae* with wide hindwings, its position is not longitudinal, but transverse or oblique, and in some cases it is eliminated by fusion of the two veins at a point. This character, then, is of no ordinal value at all. However, it should be noted that the *Hepialidae* do actually possess all those cross-veins which are generally regarded as Trichopterous, *viz.*, *hm*, *r-m*, *m cu*, *cu-a*, and *ia*; they also possess the inter-median cross-vein (*im*) which joins M_{1+2} to M_3 , and which is found in most archaic Trichoptera, though not in *Rhyacophila*. They do not possess the inter-radial cross-vein (*ir*) which joins R_{2+3} to R_{4+5} ; this occurs in most archaic Trichoptera, but not in *Rhyacophila*; in *Micropterygidae* it is confined to *Sabatinea* and *Micropteryx*.

Though the presence or absence of cross-veins cannot be used as a character of ordinal value, yet we are bound to notice another character, about which Professor Comstock is significantly silent, though it is well known to all students of the Trichoptera. I refer to the presence of the unique "wing-spot," in the angle of the fork made by R_4 and R_5 , in both wings. Dr. Ulmer, who has examined more Trichoptera than any man living, says of this wing-spot (12, p. 16):—"Allen Trichopteren, und zwar auf beiden Flügelpaaren, ist ein dunkler, horniger Punkt (Flügel-punkt) eigentümlich, welcher sich an der Basis der zweiten Apicalgabel, oder wenn diese nicht entwickelt ist, doch in der entsprechenden Region, findet; nur bei Hydroptiliden habe ich diese Punkte nicht sehen können." Putting aside, then, the highly specialised and reduced *Hydroptilidae*, which cannot be brought into any discussion upon the relationships of the *Micropterygidae*, we have this outstanding test to apply:—Do the

Micropterygide possess this wing-spot, which all other archaic Trichoptera possess, and *no other insects?* The answer is, that they do not; and hence they are not true Trichoptera. Professor Comstock must surely explain away this discrepancy before we could possibly consider the acceptance of his conclusions. Seeing that this wing-spot is visible even in the known fossil Trichoptera, we are bound to insist on its importance as an essential character of the Archetype and of all archaic members of the Order Trichoptera.

There are really four important ordinal differences between the wings of Trichoptera and Lepidoptera:—

- (a) In all archaic Trichoptera, M_1 exists as a separate vein in the forewing. In archaic Lepidoptera, M_1 is either absent, or fused with Cu_{1a} .
- (b) In all Trichoptera except only the highly reduced *Hydroptilide*, the characteristic *wing-spot* is present. It is never found in Lepidoptera.
- (c) In all Trichoptera, the tracheation of the pupal wing is reduced to two tracheæ only. In all Lepidoptera, the tracheation remains complete.
- (d) In Trichoptera, scales only appear in a few isolated and highly specialised genera, and are then of only very primitive, elongated, narrow form, with few striæ. In Lepidoptera, scales of a broad, specialised form, with numerous striæ, occur throughout the Order, from the lowest to the highest forms.

Now, in the whole of the *Micropterygide*, M_1 is *not* present as a separate vein of the forewing; the characteristic Trichopterous wing-spot is absent; the pupal wing-tracheation is complete; and scales of a broad form, with numerous striæ, are present. On all four characters, then, the *Micropterygide* must be adjudged to be archaic Lepidoptera, and not archaic Trichoptera.

Functional frenula have yet to be found in the Trichoptera. Their presence, then, in *Micropterygide* is an additional argument in favour of the non-Trichopterous nature of these insects. As true frenula occur in the Orders Mecoptera, Planipennia, and Lepidoptera, and a true jugal lobe, resembling that of *Rhyaco-*

phila, in certain Megaloptera as well as in some Trichoptera (by no means in all), it is clear that the presence or absence of these structures does not determine the Order to which the *Micropterygidae* are to belong; it only marks them as archaic.

(3) *Are the Micropterygidae true Lepidoptera?*

As this question is clearly the alternative to (2), the arguments used against (2) are those that tell in favour of (3). Hence there is no need to repeat them. We have already shown that (a) the general venational scheme might be regarded with equal reason as either Trichopterous or Lepidopterous; and (b) judged by four outstanding wing-characters, the *Micropterygidae* are most certainly archaic Lepidoptera.

It is only necessary to add that the wings do not exhibit a single character inconsistent with the inclusion of this family within the Order Lepidoptera.

While the final decision still rests to a large extent upon characters to be studied in the other parts of this paper, yet it will be seen that the study of the wings yields results that are strongly in favour of the Lepidopterous nature of the *Micropterygidae*. It is also strongly in favour of the unity of the group as a whole, either as a single family *Micropterygidae*, as Meyrick holds them to be, or as three separate but closely allied families, forming the division Jugo frenata of the Suborder Homoneura. The choice between these two alternatives rests, of course, not only upon the wing-characters, but upon the differences to be found in the mouth-parts, and the larval and pupal forms. It is, however, quite feasible to give good definitions, on wing-characters only, for the determination of these three families, if it should be found finally necessary to adopt them, as follows:—

- (1) Family *Micropterygidae* (s.str.):—Wings sharply pointed and very symmetrical about their longitudinal axes; costal area of forewing enlarged and crossed near its middle by an oblique branch from Sc. Original dichotomous branching of Rs preserved. Scales *without* scalloping of distal border, cross striolation, enclosed pigment, and coarsened longitudinal striae. Jugal lobe small, bent under forewing; a patch of short, stiff spines placed just distad from it to help in the holding of the frenulum.....
(Genera *Micropteryx*, *Sabatinea*, *Micropardulis*, *Epimartyria*).

- (2) Family *Eriocraniidæ*.—Wings more normally shaped, less pointed and symmetrical; costal area of forewing not enlarged, and not crossed by an oblique branch of Sc near its middle. Original dichotomous branching of Rs usually lost (sometimes preserved in *Mnemonicæ*). Scales closely resembling those of (1). Jugal lobe large, projecting outwards from forewing, so as to overlap the costa of the hind from above; a patch of short, stiff spines placed well distad from it.
 (Genera *Eriocrania*, *Mnemonicæ*, *Neopsenstis*).
- (3) Family *Mnesarchoidæ*.—Wings sharply pointed and symmetrical as in (1), but without any very definite enlargement of the costal area of the forewing, and with no branch of Sc in either wing. Original dichotomous branching of Rs lost, and one of the original four branches of this sector absent from both wings. Scales very highly specialised, with the distal border scalloped; cross-striolation, pigment granules, and coarsened longitudinal striae, all present. Jugal lobe and frenulum both much reduced in size, the former turned under the forewing, as in (1). (Genus *Mnesarchura*).

In defining the Division JUGO-FRENATA of the Suborder HOMONEURA of the LEPIDOPTERA (9, p.315), I gave the following characters:—

“With archaic jugo-frenate coupling apparatus consisting of jugal lobe, humeral lobe and frenulum: the jugal lobe turned under the forewing, and acting as a retinaculum for the frenulum.”

This definition will only apply strictly to the family *Micropterygidæ* (s.str.), since we now see that, in *Mnesarchura*, the jugal lobe and frenulum are so reduced as to be only doubtfully functional, while in the *Eriocraniidæ* the jugal lobe is not turned under the forewing, and does not engage the frenulum. I therefore suggest an emendation of the definition, by the omission of the second portion of the statement. The definition of the JUGO-FRENATA will then read:—

“With archaic jugo-frenate coupling apparatus consisting of jugal lobe, humeral lobe and frenulum.”

This definition will hold for the whole group *Micropterygidæ* (sens. lat.), in whatever Order it may be finally determined that they should be placed.

BIBLIOGRAPHY.

(A Bibliography will be supplied with each Part, the numbers running consecutively; but only those papers referred to in any given Part will be placed in the Bibliography for that Part).

1. CHAPMAN, T. A., 1894.—“Some Notes on the Micro-lepidoptera whose larvæ are external feeders, and chiefly on the early stages of *Eriocephalia calthella* (*Zygænida*, *Limacodida*, *Eriocephalida*). Trans. Ent. Soc. London, 1894, pp.335-350.
2. —————, 1917.—“*Micropteryx* entitled to ordinal rank; Order Zengloptera.” Trans. Ent. Soc. London, 1916 (1917), Parts iii., iv., pp.310-314, Pl. lxxxi.-xcii.
3. COMSTOCK, J. H., 1918.—“The Wings of Insects.” Comstock Publishing Co., Ithaca, N.Y., 1918.
4. FORBES, W. T. M., 1914.—“The North American Families of Lepidoptera.” *Psyche*, 1914, xxi., No.2, pp.53-65, Fig.1.
5. KELLOGG, V. L., 1894.—“The Taxonomic Value of the Scales of the Lepidoptera.” *Kansas Univ. Quarterly*, 1894, 3, pp.45-89, Pls.9-10, figs.1-17.
6. MEYRICK, E., 1912.—“Fam. *Micropterygidae*.” *Genera Insectorum*, Fasc. 132, pp.1-9, Pl. i.
7. PACKARD, A. S., 1895.—“Monograph of the Bombycine Moths of North America.” *Mem. Nat. Acad. Sciences*, Washington, 1895, vii., No.1, pp.5-390.
8. SHARP, D., 1909.—“Insects, Part ii.”, Cambridge Natural History. MacMillan & Co., London, p.433.
9. TILLYARD, R. J., 1918.—“The Panorpid Complex. Part i. The Wing-Coupling Apparatus, with Special Reference to the Lepidoptera.” *Proc. Linn. Soc. N. S. Wales*, 1918, xliii., Part 2, pp.298-301, fig.10, also Pl. xxix., figs.1-4.
10. —————, 1918.—“The Panorpid Complex. Part ii. The Wing-Trichiation, and its Relation to the General Scheme of Venation.” *Ibid.*, 1918, xliii., Part 3, pp.626-657.
11. TURNER, A. J., 1916.—“A new Micropterygid from Australia.” *Trans. Ent. Soc. London*, 1915 (1916), Parts iii., iv., pp.391-393.
12. ULMER, G., 1907.—“Trichoptera.” *Genera Insectorum*, Fasc. 60a, 60b, pp.1-259, 41 Plates.

EXPLANATION OF PLATE III.

Fig.1.—Left fore- and hindwings of pupa of *Eriocrania semipurpurella* Steph., to show tracheation and the pale banding which precedes the imaginal venation; ($\times 40$). Photographed before dissection, the wings being raised away from the body upon a glass slide, whose edge is seen crossing the lower right-hand corner obliquely.

Fig.2.—Right forewing of same, dissected off; distal two-thirds of wing only; ($\times 60$).

Fig.3.—A small portion of the basal part of the same wing as in Fig.2 ($\times 155$), to show the cubital fork (a little above the actual centre of the photograph).

(Two photographs of the fusion of Cu_2 with 1A in the hindwing were also taken at same enlargement as that of Fig.3, but the tracheæ are unfortunately slightly out of focus, and cannot be reproduced sufficiently well for publication).

LETTERING OF TEXT-FIGURES.

A, anal veins or tracheæ; 1A, 2A, 3A, first, second, and third analis respectively; *af*, anal furrow; Cu, cubitus; Cu_1 , first cubitus, dividing distally into Cu_{1a} and Cu_{1b} ; Cu_2 , second cubitus; *ca-a*, cubito-anal cross-vein; *cuf*, cubital fork; *fr*, frenulum; *hm*, humeral cross-vein; *ia*, inter-anal cross-vein; *jj*, jugum; *jl*, jugal lobe; *k*, point of fusion of Cu_2 with 1A; M, media; M_1 - M_4 , its branches; *m-cu*, medio-cubital cross-vein; *mf*, median fork; *pa*, posterior areculus; R, radius; R_1 , its main stem dividing into R_{1a} and R_{1b} distally in *Mnemonica* and in forewing of *Eriocrania*; R_s , radial sector; R_2 - R_5 , its branches; *r-m*, radio-median cross-vein; *sa*, sub-anal cross-vein; Sc, subcosta; Sc_1 , Sc_2 , its two branches in *Sabatinca* and *Micropteryx*; *sc-r*, subcosto-radial cross-vein.